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COMMENTS ON DISTRIBUTION AND NATURAL HISTORY OF POCKET GOPHERS ON THE ROLLING PLAINS OF WEST-CENTRAL TEXAS

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The Rolling Plains of Texas constitute a significant physiographic area, one that extends from the eastern escarpment of the Llano Estacado eastward, generally between the Red and Colorado rivers, to the place it meets the Cross Timbers and Prairies District (McMahon *et al.*, 1984). It merges with the latter, almost imperceptibly, at the border of the prairie lands adjacent to West Cross Timbers. Thus, although difficult to locate precisely on the ground, the eastern border of the Rolling Plains approximates the 99th meridian. Ecologically, the region more or less conforms with the Mesquite Plains Biotic District of the Kansan Biotic Province (Blair, 1954).

Dalquest and Horner (1984) accounted for mammalian species inhabiting the northeastern and north-central parts of the Rolling Plains in Texas, but the southern part of the district has received little attention from a mammalogical perspective. The survey of mammals of Coke County by Simpson and Maxwell (1989) and the study of gopher distribution in several counties by Thornton and Creel (1975) are among the exceptions to this generalization. See also Davis (1974) and Hall (1981) for overall distributional patterns.

Our object was to document the species of pocket gophers occurring in a 15-county area (see Figs. 1-2) in the southern part of the Rolling Plains and the immediately adjacent parts of the Llano Estacado, and to examine factors relating to their distribution. At the onset of our study, there was the possibility that three genera of geomyids might be en-

countered. A few reports of the plains pocket gopher, *Geomys bursarius*, already were on record (Davis, 1974; Thornton and Creel, 1975). *Cratogeomys castanops*, the yellow-faced pocket gopher, was known from the Llano Estacado along the western border of our study area and also to the south (Hollander, 1990), but not from east of the Llano escarpment at that latitude. And finally, *Thomomys bottae*, one of the smooth-toothed pocket gophers, has been reported from the Edwards Plateau to the south (as near as northwestern Tom Green County—see Hollander *et al.*, 1987). As it turned out, two of the three species are found on the southern part of the Rolling Plains.

METHODS AND ACKNOWLEDGMENTS

Beginning in the summer of 1990 and continuing to February of 1992, we drove literally hundreds of miles along roadways in the 15 counties that comprised our primary area of study. We also investigated sites in counties adjacent to our area, especially to the east and south. As we drove, we mapped location of pocket gopher mounds, pausing to set Macabee or Victor traps in areas of special interest. As have others, we found locating burrow systems much easier in winter and early spring, when most vegetation is dead or dormant, than at other times of the year.

We searched along both federal and state highways as well as Texas farm-to-market roads in quest of gophers, and occasionally along unimproved county roads. Highway rights-of-way frequently are the only localized places where pocket gophers occur, the surrounding areas being devoted to agricultural production and thus unsuited for all but ephemeral pocket gopher habitation. On the other hand, rights-of-way also could serve as corridors of dispersal for gophers, especially when suitable "fill" is hauled in to establish the road bed. To what extent road-building activities benefit pocket gophers has not been studied in detail. Certainly rights-of-way provide havens for them, but this simply may result in larger or somewhat more continuously distributed populations than otherwise would be the case. There is no evidence of which we are aware of any significant distributional shifts by gophers in which roadways were used as a means of dispersal, although Moulton *et al.* (1983) documented local movements by *Geomys bursarius* along roadsides in southeastern Colorado.

Specimens were prepared as standard museum skins accompanied by skulls. Frozen tissues were saved from some. All specimens and

tissues are housed in The Museum at Texas Tech University. Measurements used in the following accounts are in millimeters and weights are in grams.

There is a soil survey for each of the 15 counties in which we searched for pocket gophers, published by the Soil Conservation Service of the U.S. Department of Agriculture. We used these extensively, not only to plot the soil types in which gophers were taken, but also in planning field work. We found them quite helpful.

We are indebted to S. D. Brown, L. L. Choate, A. F. Laemmerzahl, R. W. Manning, and F. D. Yancey for assistance in the field. Clyde Hendrick, Dean of the Graduate School at Texas Tech University, and Gary Edson, Director of The Museum, provided financial aid for travel. Additionally, one of us (Goetze) held a Graduate School Research Assistantship in the summer of 1990 when the project was initiated. R. D. Bradley and R. J. Baker provided karyotypic data and R. M. Timm identified lice.

RESULTS

Cratogeomys castanops

The yellow-faced pocket gopher is widely distributed on the Llano Estacado (Hollander, 1990). In the 15-county area, it occupies sandy to clayey loams, frequently with conspicuous calcareous content, in the west in Borden, Dawson, Howard, and Lynn counties, and east of the Llano in Borden, Howard and Scurry counties (Fig. 1). Gophers from atop the High Plains are assignable to the subspecies *C. c. perplanus*, whereas those to the east of the escarpment are referable to the race *C. c. dalquesti*.

On the Llano, most land turned for agriculture is devoted to growing cotton. Not only does this result in narrow rights-of-way (no fencing) along many farm-to-market and county roads, but such a monoculture does not allow much utilization of agricultural lands by pocket gophers. Consequently, *Cratogeomys* (and northwardly *Geomys*) frequently are concentrated along state and federal highways. On the Rolling Plains to the east of the Llano in Borden, Howard, and Scurry counties, a significant amount of mesquite grassland, utilized for range cattle, still prevails, but *C. castanops* seems nonetheless to be concentrated along roadways. It must penetrate the grassland areas as well, although we have seen little evidence of this. Nor have we found at any place the situation described by Moulton *et al.* (1983) in Colorado

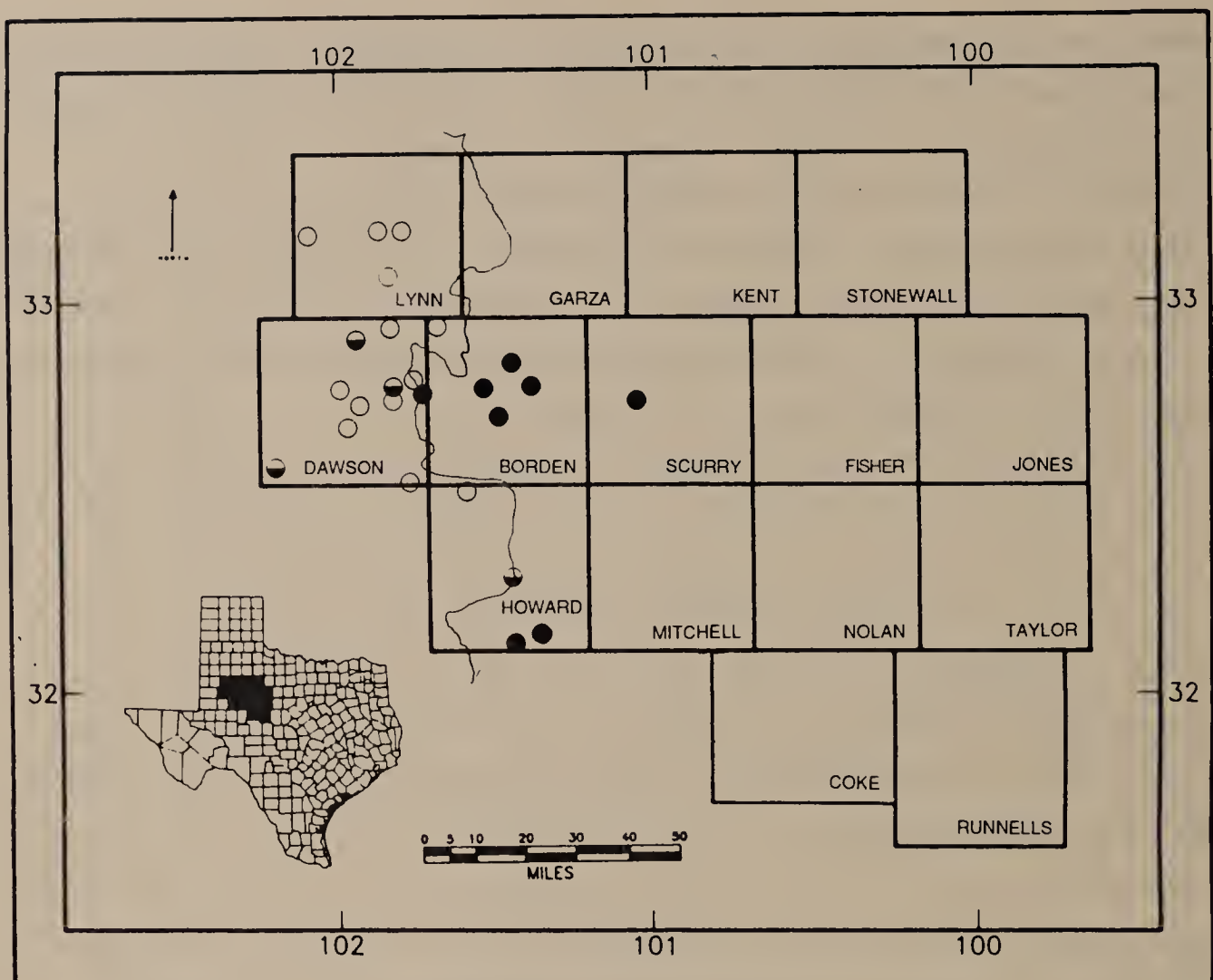


FIG. 1.—Records of *Cratogeomys castanops*. Solid symbols represent specimens of *C. c. dalquesti*; open symbols represent specimens of *C. c. perplanus*, whereas half-solid symbols represent reports in the literature of that subspecies. The north-south line through the western counties represents the approximate border between the High Plains (Llano Estacado) and Rolling Plains.

where *Geomys* was found in bar ditches along roadways and *Cratogeomys* was taken nearby in native rangeland. In fact, we found no place in the 15-county area where the local distribution of the two species came into close proximity, as is known elsewhere within their ranges. *Geomys* prefers deep, sandy soils, evidently excluding *Cratogeomys* from such areas. The latter normally occupies harder, more calcereous soils of clay or clay-loam, but is found in sandy areas in the absence of plains pocket gophers. In our study area, for example, *Geomys* is found in northeastern Lynn County but *Cratogeomys* abounds to the south and west, and *Geomys* occurs to the north, south, and east of Snyder, Scurry County, with *Cratogeomys* found to the west of Snyder.

Soils in areas inhabited by *C. c. perplanus* in southern Lynn, Dawson, adjacent Borden, and northern Howard counties are composed primarily of Amarillo series elements. These are soils of the Llano Estacado

that developed in loamy alluvium and eolian materials, usually formed over caliche.

Cratogeomys castanops dalquesti from Borden, Dawson, and Scurry counties, to the east of the Llano Estacado, represent a northward extension of the known range of this subspecies. Animals from Borden County were found in Olton-Rowena-Rotan association soils, which are deep and have a clay-loam surface over clay. Soils of this association were formed from loamy outwash and eolian materials. A specimen from Scurry County was taken in a soil zone of the Olton clay-loam series, whereas those from southern Howard County inhabited Portales clay-loam soils.

According to Hollander (1990), *C. c. dalquesti* differs from *C. c. perplanus* in being smaller cranially, slightly darker in color, and in having a broader and uniquely shaped lacrimal bone. Nine adult females of *perplanus* from Borden, Dawson, and Lynn counties had the following external measurements (average followed by extremes): total length, 286.1 (273-309); length of tail, 75.1 (66-86); length of hind foot, 37.8 (36-42); length of ear, 7.5 (6-8). Eight of these animals (all nonpregnant) weighed an average of 307.6 (287.6-332.5). Measurements of two adult females of *C. c. dalquesti* from southern Borden County were 272, 268; 80, 64; 39, 37.5; 7, 7. Weights were 275.0 and 270.0, respectively. Cranial measurements are listed in Table 1.

The yellow-faced pocket gopher is reproductively active the year around in western Texas and adjacent New Mexico (Davidow-Henry *et al.*, 1989). From our study area, we have records of gravid females collected in February (two fetuses x 27 in crown-rump length), May (two x 30 and three x 42), and November (two x 38). A lactating female was obtained in April and another with swollen uteri in January. A May-taken adult male had testes that measured 25 x 9. Lack of additional reproductive data is due, in part at least, to the effects of seasonal sampling.

Geomys bursarius

Sandy soils, specifically fine sandy loams, are favored by *Geomys bursarius major*, which evidently excludes *C. castanops* from such habitats. Within the range of the plains pocket gopher in our study area, this species inhabits Miles fine sandy loam in all but Coke, Jones, Nolan, and Runnels counties. This soil was formed in sandy outwash or old alluvium. The surface layer is a brownish and fine sandy loam

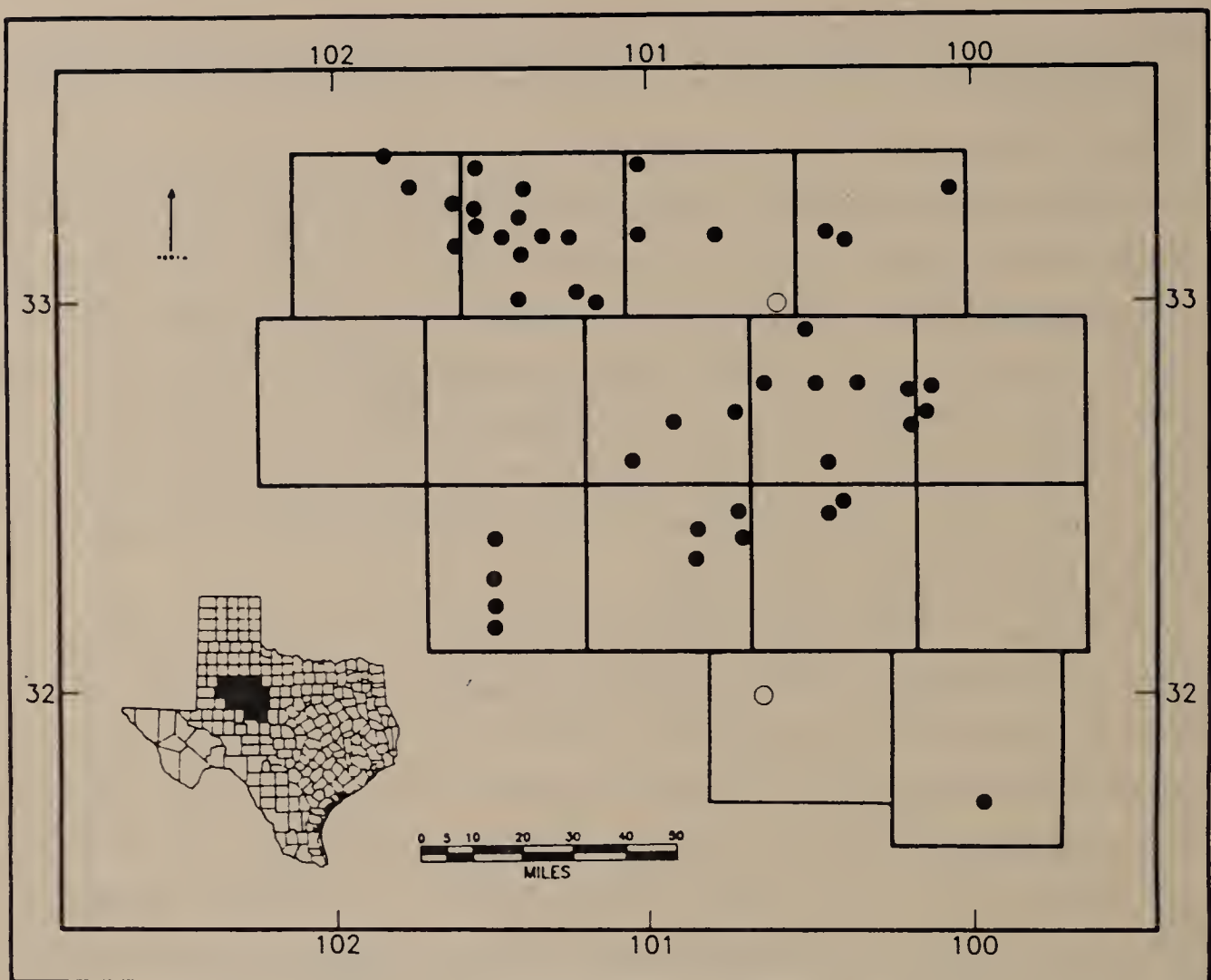


FIG. 2.—Records of *Geomys bursarius major*. Solid symbols represent specimens examined, whereas open symbols represent records from the literature. See Figure 1 for names of counties.

that averages 10 inches in thickness and was developed over a layer of friable, sandy clay-loam, which is, on average, 70 inches thick. Specimens from Jones County were collected from a small pocket of Winters fine sandy loam located at the western edge of that county, whereas those from Nolan County inhabited a different fine sandy loam classified in the Paducah-Woodward series.

No gophers were taken in Taylor County, where most soils are calcareous clays and clayey loams that are shallow and stony, clearly unsuitable for *G. bursarius*. This is true also of all but extreme western Jones County, most of Fisher and Nolan counties, southern Mitchell County, and Stonewall County from Aspermont eastward. Some of these areas are dominated by rough, broken land that is characterized by steep slopes and shallow, rocky, and erodible soils.

In Runnels County, at the southeastern edge of our study area, there is an isolated population of *G. bursarius* to the south of the Colorado River just southwest of Ballinger. Gophers were first taken in this area in 1971, when Thornton and Creel (1975: 274) trapped specimens “in

areas of deep sand” above the floodplain of the river along U. S. Highway 67. We returned to this place in 1991 and found *G. bursarius* mounds common along the divided highway and its access roads, and to either side of the access roads, from approximately two to four miles southwest of Ballinger. Insofar as we could tell, gophers inhabited an area a few hundred yards to either side of the access roads, perhaps as much as a mile to the north. Rangeland and several small vineyards were adjacent to the highway. One farmer-rancher, who has lived in the immediate area since 1952, reported that the animals were common there when he purchased his present property. The localized sandy soil is Tivoli-Brownfield, which has a surface layer of fine, pale brown sand that is 20 to 40 inches deep, deposited over a reddish, sandy-clayey loam that may be as deep as 50 inches. *Geomys bursarius* seems to be excluded from other areas in Runnels County due to the shallow, rocky nature of soils both north and south of Ballinger, nor did we find gophers in counties to the east of Runnels.

To the southwest of Ballinger, the distribution of *G. bursarius* stopped abruptly when Tivoli-Brownfield sand gave way to Acuff loam. To the north, in good years, the distribution of these gophers evidently extends all the way to the Colorado River and perhaps beyond, because in February of 1986 one of us (Jones) noted active mounds along State Highway 158 on the northwestern outskirts of Ballinger. These were completely gone a month later when a field party returned to trap there, demonstrating once again the rapidity by which a local area can be inhabited by gophers and then abandoned. Along U. S. Highway 67, Tivoli-Brownfield sands are surrounded in part by sandy loams of the Miles series, soils in which *Geomys* also sometimes is found.

The presence of plains pocket gophers south of the Colorado River in Runnels County immediately raises the question of their relationship to gophers referred to as *Geomys texensis* that occur in a similar situation about 100 miles southeastward. However, our specimens closely resemble those of *G. b. major* listed herein in external and cranial morphology. Furthermore, they have the karyotypic characteristics of *major* (as do specimens from farther north in Fisher County) as opposed to *texensis* (see Block and Zimmerman, 1991), and were parasitized by a louse, *Geomydoecus oklahomensis*, that is typical of *major* and its allies rather than *G. heaneyi*, which parasitizes *texensis* (Timm and Price, 1980). Nor are the specimens from near Ballinger in

any way reminiscent in external, cranial, or karyotypic characters of *Geomys knoxjonesi*, which occurs on the southwestern part of the Llano Estacado and in adjacent areas some 150 miles or so to the west.

Average (and extreme) external measurements of eight adult females from Runnels County followed by those of eight from Garza County are: total length, 245.9 (238-256), 247.5 (235-260); length of tail, 74.2 (71-78), 69.2 (58-79); length of hind foot, 30.7 (30-32), 30.0 (29-31); length of ear, 6.0 (5-7), 5.9 (5-8). Seven nonpregnant females from Runnels County averaged 181.0 (155-205) in weight, whereas seven from Garza County averaged 183.1 (160-210). For cranial measurements, see Table 1.

As for the locality in Coke County, Thornton and Creel (1975) collected two *G. bursarius* in sandy soil along the Colorado River in 1971—at Willcoxson Ranch, 10 mi. NW Robert Lee (Simpson and Maxwell, 1989). We have been unable to determine on which side of the Colorado these specimens were taken, but we presume on the north because Tivoli-Brownfield sandy soil prevailed there as it does today. The dam of E. V. Spence Reservoir, northwest of Robert Lee, was closed in 1969, but the lake filled slowly and, in fact, is not yet completely filled. It is possible that areas in which *G. bursarius* once occurred now have been inundated by the rising water level. There are, nonetheless, several extant, albeit small, areas of Tivoli-Brownfield sand on the north side of the Colorado where plains pocket gophers still may occur. We searched for them in vain, however, in northwestern Coke County along FM 2059 and State Highways 158 and 208.

A gopher from northeastern Stonewall County was obtained along the Salt Fork of the Brazos River. Soil in this area is alluvial, fine sandy loam and loamy fine sand, both favorable to habitation by *Geomys*. Gophers from northeastern Stonewall County inhabited soils classified as Lincoln series loamy fine sands.

To the west, we took no *G. bursarius* in Borden or Dawson counties, only *Cratogeomys*, and the latter occupies all but the northeastern fourth of Lynn County as well. Calcareous soils prevail in these areas—soils in which *Geomys* does not occur. Thus, *G. bursarius* is distributed on the southern Rolling Plains as an ever narrowing wedge from the north, culminating in the isolated populations in Coke and Runnels counties.

We have records of pregnant females from the months of January, February, March, and November; seven carried an average of 3.8 (two

TABLE 1.—*Cranial measurements of selected specimens of two species of pocket gophers from the Texas Rolling Plains and adjacent areas, illustrating size relationships among populations. All specimens are adults (age classes 4 and 5 as defined by Hollander, 1990:14). Measurements were taken to the nearest hundredth of a millimeter, using Fowler digital calipers, then rounded to the nearest tenth of a millimeter.*

Catalogue number or number of specimens averaged, and sex	Condylobasal length	Zygomatic breadth	Mastoid breadth	Length of rostrum	Breadth of rostrum	Postorbital constriction	Palatofrontal depth	Length of max. toothrow
<i>Geomys bursarius major</i> , Garza-Kent counties, Texas								
Average 9 (F)	41.91	25.74	24.08	18.19	10.10	6.18	15.67	8.42
Minimum	41.0	25.1	23.0	17.5	9.5	5.8	15.3	8.0
Maximum	43.1	26.6	24.9	19.0	11.2	6.7	16.2	9.2
Jones-Fisher-Stonewall counties, Texas								
TTU 59172, F	42.0	25.7	23.6	18.5	10.0	5.8	15.9	8.6
TTU 50179, F	44.5	—	26.0	18.9	10.8	6.8	17.0	8.6
TTU 59188, F	42.3	26.4	25.0	18.7	10.1	5.8	16.0	8.8
Runnels County, Texas								
TTU 59192, F	42.2	26.8	25.7	18.8	10.2	6.7	15.7	8.1
TTU 59194, F	42.7	—	25.1	19.2	10.1	6.9	15.3	8.5
TTU 59195, F	43.4	—	24.6	18.8	10.5	6.5	15.7	8.4
TTU 59196, F	43.8	27.8	25.5	19.8	10.8	7.3	16.1	8.7
<i>Cratogeomys castanops perplanus</i> , Dawson County, Texas								
TTU 25268, M	59.9	41.1	35.6	27.4	13.9	7.5	24.1	11.2
TTU 25278, M	61.3	44.3	35.2	27.5	14.3	7.3	24.1	11.3
TTU 25270, F	53.1	34.2	29.7	23.5	12.0	6.6	20.8	9.7
TTU 25291, F	53.4	34.0	31.2	22.7	12.0	6.9	20.5	9.7
TTU 26034, F	53.4	33.9	30.5	23.2	11.3	6.8	20.0	10.5
<i>Cratogeomys castanops dalquesti</i> , Borden County, Texas								
TTU 59139, M	58.2	39.8	32.4	25.6	12.9	7.0	22.5	10.8
TTU 60396, M	58.7	39.4	33.5	26.8	13.9	6.7	23.2	10.7
TTU 60405, M	58.2	39.1	34.5	26.1	12.9	7.0	21.9	9.9
TTU 59169, F	52.7	33.2	29.8	23.5	11.0	7.0	20.3	9.5
TTU 59393, F	50.5	32.7	28.6	22.4	10.9	6.7	19.8	9.0
TTU 60404, F	52.2	34.6	29.8	24.9	11.2	7.3	20.2	10.5

to five) fetuses. Females taken in December and April evinced no reproductive activity. Males with scrotal testes were captured in January (20 x 13, 17 x 12, 24 x 14, and 20 in length), February (25 x 14, and 20 x 14), March (20 x 15), April (22 x 14), May (15 x 8), and November (20 x 11).

SPECIMENS EXAMINED

We examined 65 *Cratogeomys castanops* and 116 *Geomys bursarius* from the 15-county study area, more than half of which were collected by us. The others had been deposited previously in the collection of mammals at The Museum of Texas Tech University or were found among pocket gophers housed in the collection at Midwestern State University (MWSU). Additionally, we have listed specimens reported in the literature from localities not otherwise represented, along with a citation to the appropriate publication.

Localities of record are shown on Figure 1 (*Cratogeomys*) and Figure 2 (*Geomys*). Some localities are not plotted because undue crowding of symbols would have resulted; these are listed in italic type below. For the same reason, a few symbols are slightly offset on the maps.

***Cratogeomys castanops dalquesti* Hollander, 1990**

Specimens examined (10).—BORDEN CO.: 10.5 mi. N Gail, 1; 7.5 mi. W Gail, 1; 5 mi. E Gail, 1; 5.5 mi. E Gail, 2; 4 mi. S, 1.5 mi. W Gail, 1. DAWSON CO.: 2 mi. S, 13 mi. E Lamesa, 1. HOWARD CO.: 11.2 mi. S Big Spring, 1 (MWSU); 13 mi. SSE Big Spring, 1 (MWSU). SCURRY CO.: 5 mi. W Union, 1.

***Cratogeomys castanops perplanus* Nelson and Goldman, 1934**

Specimens examined (55).—BORDEN CO.: 11 mi. N, 13.5 mi. W Gail, 2; DAWSON CO.: 2 mi. S, 1 mi. W O'Donnell, 2; 4 mi. S, 4 mi. E O'Donnell, 1; 5 mi. S, 1 mi. E O'Donnell, 2; Lamesa, 1 (MWSU); 2.2 mi. S, 0.3 mi. E Lamesa, 2; 2.3 mi. S Lamesa, 7; 2.8 mi. S, 0.6 mi. E Lamesa, 2; 2.9 mi. S Lamesa, 4; 3.3 mi. S, 4 mi. E Lamesa, 5; 4.6 mi. S, 4.3 mi. E Lamesa, 1; 5 mi. ENE Key, 1; 4 mi. WSW Key, 1; 5 mi. S, 4.5 mi. E Lamesa, 5; 5.2 mi. S, 5 mi. E Lamesa, 1; 6 mi. S, 5.7 mi. E Lamesa, 4; 6.8 mi. S, 1.3 mi. E Lamesa, 5; 1 mi. NNW Ackerly, 1. HOWARD CO.: 1.5 mi. WSW Vealmoor, 1. LYNN CO.: 1 mi. E West Point, 1; Tahoka, 1 (MWSU); 2.5 mi. E Tahoka, 1; 4 mi. E Tahoka, 1; 10 mi. S, 2 mi. E Tahoka, 3.

Additional records (Hollander, 1990: 54).—DAWSON CO.: 11.1 mi. N, 3 mi. E Lamesa; 11.1 mi. N, 4.3 mi. E Lamesa; 10 mi. E Lamesa; 22 mi. SW Lamesa. HOWARD CO.: Big Spring. LYNN CO.: 3 mi. S Tahoka.

Geomys bursarius major Davis, 1940

Specimens examined (116).—FISHER Co.: 6 mi. NW Rotan, 1; 12.5 mi. W Roby, 1; 5 mi. W Roby, 1; 10 mi. E Roby, 1 (MWSU); 6 mi. S, 1 mi. E McCaulley, 2; 3 mi. E Sylvester, 1; 2 mi. S, 3.5 mi. E Sylvester, 2; 9.5 mi. N Sweetwater, 1. GARZA Co.: 5.5 mi. SE Southland, 1; 10 mi. N Post, 1; 8 mi. N, 8.5 mi. W Post, 1; 7 mi. N Post, 7; 5 mi. N, 6.5 mi. W Post, 1; 4.5 mi. NW Post, 1; 3 mi. NW Post, 3; 2 mi. E Post, 2; 11.5 mi. E Post, 2; 0.5 mi. S, 8.5 mi. W Post, 1; 0.5 mi. S, 3 mi. W Post, 1; 5.5 mi. S, 0.5 mi. W Post, 1; 0.5 mi. N, 1.5 mi. E Justiceburg, 1; 0.3 mi. N, 0.5 mi. E Justiceburg, 1; 4 mi. E Justiceburg, 2; 0.25 mi. SE Justiceburg Post Office, 1; 13.5 mi. S, 1 mi. W Post, 1; 14 mi. S, 1 mi. E Post, 1; 6 mi. SE Justiceburg, 1. HOWARD Co.: 9 mi. N Big Spring, 1; 2 mi. N Big Spring, 1; 2.1 mi. NE Big Spring, 2; Big Spring, 2; 5.6 mi. S Big Spring, 1 (MWSU); 7.6 mi. S Big Spring, 1 (MWSU); 8.7 mi. S Big Spring, 1 (MWSU); 9.2 mi. S Big Spring, 1 (MWSU). JONES Co.: 4.5 mi. S, 2 mi. E Hamlin, 1; 9 mi. S, 0.5 mi. W Hamlin, 2. KENT Co.: 2 mi. N, 26 mi. W Girard, 2; 26 mi. W Girard, 1; 1 mi. N, 15.5 mi. W Clairemont, 1; 2 mi. W Clairemont, 1; 1.9 mi. E Clairemont, 1. LYNN Co.: 14 mi. N Tahoka, 2; 10.5 mi. N Grassland, 1; 8 mi. N, 1.5 mi. E Grassland, 1; 2 mi. S, 2 mi. W Wilson, 1; 12 mi. E Tahoka, 1; 1 mi. E Grassland, 1; MITCHELL Co.: 3 mi. N, 0.3 mi. E Colorado City, 9; 4 mi. N Loraine, 3; 4 mi. S, 0.5 mi. E Loraine, 1; 5 mi. S, 2 mi. E Colorado City, 1. NOLAN Co.: 3 mi. E Sweetwater, 3; 4 mi. E Sweetwater, 1; 2 mi. S Sweetwater, 1; 3 mi. S Sweetwater, 1. RUNNELS Co.: 3 mi. SW Ballinger, 14. SCURRY Co.: 4 mi. E Snyder, 1; 1 mi. S, 4 mi. E Snyder, 1; 2 mi. S, 1 mi. E Snyder, 1; 4 mi. SW Snyder, 1 (MWSU); 4 mi. S Snyder, 1; 5 mi. N, 4 mi. E Hermleigh, 1; 1 mi. N, 4 mi. W Ira, 4. STONEWALL Co.: 10 mi. W Rochester, 1 (MWSU); 2.5 mi. N, 7 mi. W Peacock, 1; 2 mi. N, 1 mi. W Peacock, 1; 0.5 mi. S, 0.5 mi. E Peacock, 3.

Additional records.—COKE Co.: 10 mi. NW Robert Lee (Thornton and Creel, 1975: 274). HOWARD Co.: 2 mi. N, 3 mi. E Big Spring (Baker *et al.*, 1973: 769). KENT Co.: 14.5 mi. NW Rotan (Baker *et al.*, 1973: 769). RUNNELS Co.: 2 mi. S[W] Ballinger (Thornton and Creel, 1975: 274).

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5 AUGUST 1992

SECONDARY SEXUAL DIMORPHISM AND
GEOGRAPHIC VARIATION IN ORD'S KANGAROO
RAT, *DIPODOMYS ORDII*, ON THE LLANO
ESTACADO AND IN ADJACENT AREAS OF TEXAS

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Ord's kangaroo rat, *Dipodomys ordii*, is widely distributed throughout much of western North America, from southernmost Canada to central México. Because of the broad range of these rats and their tendency to form semi-isolated populations, this species is an ideal subject for the study of geographic variation (Schmidly, 1971). Setzer (1949) examined intraspecific variation in *D. ordii*; he recognized 35 subspecies, which he grouped into six complexes. His Great Plains complex included seven races, two of which, *D. o. medius* and *D. o. richardsoni*, were recorded as occurring on the Llano Estacado of Texas and eastern New Mexico. Hall (1981) arbitrarily mapped the boundary between these two taxa (*D. o. richardsoni* to the north and *D. o. medius* to the south) through the middle of the Llano Estacado, although no obvious biogeographic barrier exists there.

The Llano Estacado is an extensive plateau encompassing approximately 35,000 square miles and is the southern extension of the Great Plains. It is located south of the Canadian River in western Texas and eastern New Mexico (Lotspeich and Coover, 1962), and is separated from adjacent areas by caprock breaks on the northern and eastern margins, and to a lesser extent on the western margin. To the south and southeast, the Llano merges with the Monahans Sandhills and the Edwards Plateau, respectively (Judd, 1970). The Llano Estacado is

topographically uniform, with no geographic features that might present a barrier to gene flow in small mammals (with the possible exception of extensive cultivation in some areas, a relatively recent development). Jones *et al.* (1988) opined that the Canadian River and its breaks could provide an area where gene flow is discontinuous between populations of *Dipodomys ordii* distributed to the north and south. If this is the case, it is possible that the breaks on the eastern boundary of the Llano provide an area of discontinuous gene flow as well. The purpose of this study was to examine patterns of geographic variation in *D. ordii* on the Llano Estacado and in adjacent areas, using multivariate statistical techniques, and to relate those patterns to natural geographic features that might restrict gene flow, thus providing a taxonomic framework for future studies of this kangaroo rat.

METHODS

Specimens examined.—Specimens of *D. ordii* used in this study from the Llano Estacado and adjacent areas in Texas are housed in The Museum, Texas Tech University. Important details relative to examination and subsequent analyses of characters are discussed below.

Sex and age classes.—Individual specimens were separated according to sex and divided into age categories (prior to taking measurements) by the following methods described by Desha (1967): *subadult*—permanent dentition incomplete (p4 not fully erupted); *young adult*—permanent dentition complete, teeth showing slight to moderate wear with cusps and primary folds present, auditory bullae rough, opaque, and porous, and basioccipital-basisphenoid suture clearly evident; *adult*—substantial wear on teeth with cusps worn relatively smooth and each tooth with a peripheral band of enamel and a lake of dentine, auditory bullae smooth, shiny, nonporous, and showing at least some translucence, and the basioccipital-basisphenoid suture ankylosed. Only adult specimens were used in analysis of secondary sexual dimorphism and patterns of geographic variation.

Measurements.—Standard external measurements—total length, length of tail vertebrae, length of hind foot, and length of ear—were recorded from original specimen labels. Due to different measuring techniques of various collectors, these measurements were not used in multivariate and univariate statistical analyses for sexual dimorphism and geographic variation, although they are included in Table 1 for information. All cranial measurements were taken by Robertson using the same pair of Fowler digital calipers that were calibrated to the nearest 0.01 mm. Cranial measurements used in this study are the same as those used by various other investigators for study of geographic variation in *Dipodomys ordii* (Desha, 1967; Schmidly, 1971; Kennedy and Schnell, 1978; Kennedy *et al.*, 1980; Baumgardner and Schmidly, 1981). Those chosen for analysis were shown to be good indicators of variation between sexes and geographic localities in the previous studies. Cranial dimensions we used are as follows: greatest length of skull, mastoid breadth, postorbital constriction, maxillary breadth, rostral breadth, length of

nasals, least supraoccipital breadth, bullar-premaxillary length, basal length, length of diastema, width of upper molar, length of maxillary toothrow, and depth of skull. These measurements have been described in detail by previous investigators (see citations above).

Analysis.—Multivariate and univariate statistical techniques were utilized to examine cranial characters for adult specimens. All statistical tests used were from programs available in the SPSS/PC+ statistical package (SPSS Inc., 1988).

Specimens from immediately adjacent localities were pooled to form samples of sufficient size for statistical analysis (Fig. 1). All specimens that were not pooled were treated as unknown in the analyses. A general description of the groups will be given in the section on geographic variation.

In all statistical analyses, multivariate tests were used to detect group differences before any univariate tests were used. It has been demonstrated that the results of numerous univariate tests do not emulate the results of a multivariate test (Willig *et al.*, 1986; Willig and Owen, 1987), and a multivariate question is asked when analyzing morphological variation in natural populations (Hollander, 1990). Specific statistical tests performed on the data will be discussed in detail in the following sections on secondary sexual dimorphism and geographic variation.

Accounts of subspecies follow the section on geographic variation and each terminates with a list of specimens examined. Localities from which specimens were examined also are plotted on Figure 1. Some localities from which kangaroo rats were studied are not plotted on the map because undue crowding of symbols would have resulted; for the same reason, a few symbols are slightly offset on the map. Also, a few localities from which specimens were available lie to the east or south of the map border. Those localities not mapped are in italic type. Localities are listed alphabetically by county; within a county, they are listed from north to south and, at the same latitude, from west to east.

SECONDARY SEXUAL DIMORPHISM

In his study of subspeciation in Ord's kangaroo rat, Setzer (1949), using small sample sizes, found sexual dimorphism to be nonsignificant. It has been found in more recent studies of *Dipodomys ordii* in western Texas, however, that sexual dimorphism was a significant factor; thus, authors analyzed sexes separately (Desha, 1967; Schmidly, 1971). Desha (1967) found significant sexual dimorphism in nine of 14 cranial characters in *D. o. medius*. He reported that sexes differed significantly in greatest length and depth of skull, basal, bullar-premaxillary, nasal, and diastemal lengths, and greatest cranial, maxillary, and least interorbital breadths.

Schmidly (1971) examined sexual dimorphism in four populations of *D. ordii* from western Texas and found significant sexual dimorphism in 14 of 26 characters in one population. He found that two of the remaining three populations were dimorphic in five characters and the fourth population dimorphic in 10. He noted that the degree of

sexual dimorphism varied geographically. From these findings, he suggested that sexes should be considered separately in further taxonomic studies of *D. ordii*. However, Baumgardner and Schmidly (1981) did not find consistent sexual dimorphism in any characters that were analyzed from 13 separate localities in southern Texas and northern México. Schmidly and Hendricks (1976) also noted only limited sexual dimorphism in cranial and external measurements of *D. ordii* from southern Texas and México.

A multivariate analysis of variance (MANOVA) was performed on a single large sample of 119 individuals from the Muleshoe Sand Hills (Bailey, Lamb, and Hale counties—group 1 of Table 1) to determine the presence or absence of secondary sexual dimorphism. The results of the MANOVA ($P = 0.035$) indicated significant differences between sexes and as a result they were separated in subsequent analyses.

Schmidly (1971) reported no significant differences between males and females in external measurements for the four populations he investigated. Although no tests for significance were utilized on external characters in the present study, the means of external measurements of the samples were similar between males and females. Males were generally larger cranially than females in all but two groups. Females from group 2 were larger than males in all characters except length of nasals and length of maxillary toothrow, and females from group 5 were larger in all characters except maxillary breadth, length of nasals, and length of diastema (Table 1).

GEOGRAPHIC VARIATION

When Setzer (1949) studied variation in *D. ordii*, he used both quantitative and qualitative characteristics to differentiate among subspecies, but the statistical significance of population variability was not presented. In addition, some of the samples used by Setzer were small. For example, he assigned 129 specimens to *D. o. medius*, but the largest sample from any one locality was 10 and the average sample size was four (Desha, 1967).

Several authors have examined geographic variation in *D. ordii* from the High Plains of Texas, New Mexico, and western Oklahoma (Desha, 1967; Schmidly, 1971; Hartman, 1980; and Kennedy *et al.*, 1980). These studies were conducted using specimens from within the ranges of three subspecies, namely *D. o. medius*, *D. o. richardsoni*, and *D. o.*

TABLE 1.—*Summary statistics for each sex for pooled samples (see Fig. 1) of Dipodomys ordii from the Llano Estacado and adjacent areas in Texas. Statistics for each group are sample size (N), mean, standard deviation (SD), standard error (SE), and range (minimum-maximum). All measurements are given in millimeters.*

Group	N	Mean	SD	SE	Range
Greatest length of skull					
Males					
1	54	39.54	0.92	0.12	36.82-41.44
2	16	39.28	0.70	0.18	38.08-40.75
3	53	39.51	0.73	0.10	37.46-41.11
4	23	39.77	0.93	0.19	38.59-41.82
5	19	39.44	0.89	0.20	37.46-40.81
6	32	40.03	0.85	0.15	37.69-41.41
Females					
1	63	39.40	1.01	0.13	36.35-41.42
2	17	39.52	1.09	0.26	37.46-41.38
3	34	39.29	0.87	0.15	37.71-41.40
4	14	39.43	0.81	0.22	38.34-41.20
5	13	39.76	1.13	0.31	37.76-41.50
6	30	40.02	0.85	0.16	38.48-41.57
Mastoid breadth					
Males					
1	56	24.57	0.60	0.08	22.97-25.92
2	16	24.55	0.41	0.10	23.54-25.37
3	53	24.64	0.60	0.08	23.30-26.41
4	23	24.64	0.57	0.12	23.69-25.90
5	20	24.69	0.79	0.18	23.23-25.80
6	32	24.43	0.62	0.11	22.93-25.90
Females					
1	63	24.61	0.66	0.08	22.82-26.11
2	17	24.74	0.75	0.18	22.96-25.90
3	36	24.56	0.68	0.11	22.98-25.71
4	15	24.59	0.73	0.19	23.55-26.42
5	14	24.70	0.67	0.18	23.32-25.78
6	30	24.43	0.54	0.10	23.23-25.65
Postorbital constriction					
Males					
1	56	13.38	0.72	0.10	12.07-16.21
2	16	12.98	0.47	0.12	12.21-13.94
3	58	13.19	0.57	0.08	11.57-14.39
4	21	13.02	0.66	0.14	11.51-14.11
5	20	12.80	0.50	0.11	11.97-13.78
6	31	13.08	0.61	0.11	11.85-14.03
Females					
1	61	13.17	0.46	0.06	12.26-14.32
2	17	13.14	0.47	0.11	12.06-13.95
3	36	13.13	0.51	0.08	12.09-14.14
4	15	13.14	0.64	0.16	12.06-14.04
5	14	13.04	0.43	0.12	12.50-13.90
6	30	13.02	0.33	0.06	12.13-13.50

TABLE 1.—Continued.

Group	N	Mean	SD	SE	Range
Maxillary breadth					
Males					
1	56	21.46	0.57	0.08	19.60-22.56
2	16	21.27	0.62	0.16	20.19-22.44
3	57	21.29	0.70	0.09	19.73-22.39
4	23	21.29	0.69	0.14	20.06-22.62
5	19	21.72	0.72	0.17	20.08-23.07
6	29	21.74	0.71	0.13	20.29-23.50
Females					
1	62	21.58	0.67	0.09	19.81-22.97
2	17	21.33	0.76	0.19	19.95-22.46
3	35	21.04	0.63	0.11	19.83-22.22
4	14	21.20	0.81	0.22	20.20-23.51
5	14	21.67	0.61	0.16	20.58-22.43
6	29	21.72	0.61	0.11	20.66-23.14
Rostral breadth					
Males					
1	56	3.88	0.25	0.03	2.90-4.46
2	16	3.59	0.22	0.05	3.59-4.28
3	51	3.91	0.23	0.03	3.35-4.42
4	23	3.72	0.24	0.05	3.26-4.15
5	20	4.03	0.27	0.06	3.59-4.45
6	31	4.11	0.20	0.04	3.73-4.55
Females					
1	63	3.91	0.23	0.03	3.34-4.43
2	17	3.96	0.18	0.04	3.57-4.28
3	35	3.98	0.23	0.04	3.52-4.68
4	15	3.78	0.17	0.04	3.39-3.96
5	14	4.12	0.25	0.07	3.79-4.67
6	30	4.01	0.16	0.03	3.76-4.43
Length of nasals					
Males					
1	54	14.48	0.68	0.09	11.68-15.45
2	16	14.56	0.58	0.14	13.86-15.71
3	53	14.49	0.47	0.06	13.62-15.96
4	23	14.43	0.58	0.12	13.56-15.94
5	20	14.52	0.48	0.11	13.85-15.51
6	32	14.49	0.46	0.08	14.13-15.88
Females					
1	63	14.53	0.57	0.07	13.24-16.16
2	17	14.54	0.44	0.11	13.73-15.29
3	34	14.34	0.60	0.10	13.11-15.80
4	14	14.20	0.53	0.14	13.13-14.94
5	13	14.44	0.83	0.23	12.73-15.52
6	30	14.82	0.52	0.10	14.10-16.11

TABLE 1.—Continued.

Group	N	Mean	SD	SE	Range
Least supraoccipital breadth					
Males					
1	56	2.63	0.41	0.05	1.78-3.63
2	16	2.65	0.49	0.12	1.80-3.58
3	60	2.50	0.38	0.05	1.44-3.54
4	23	2.44	0.35	0.07	1.79-3.31
5	20	2.78	0.32	0.07	2.20-3.40
6	31	2.88	0.39	0.07	1.79-3.68
Females					
1	63	2.56	0.41	0.05	1.58-3.44
2	17	2.76	0.45	0.11	2.20-3.78
3	35	2.53	0.32	0.05	1.87-3.37
4	15	2.50	0.45	0.12	1.79-3.25
5	14	2.87	0.47	0.13	2.03-3.67
6	30	3.01	0.37	0.07	2.23-3.62
Bullar-premaxillary length					
Males					
1	56	36.52	0.83	0.11	34.37-38.47
2	16	36.27	0.69	0.17	35.07-37.49
3	55	36.54	0.65	0.09	35.30-38.33
4	23	36.63	0.84	0.18	35.55-38.28
5	19	36.54	0.85	0.20	34.84-38.15
6	27	37.16	0.70	0.14	35.78-38.30
Females					
1	62	36.48	1.08	0.14	33.49-39.28
2	16	36.47	0.95	0.24	34.85-38.24
3	35	36.22	0.85	0.14	34.80-38.41
4	15	36.38	0.67	0.17	35.04-37.34
5	14	36.73	1.04	0.28	35.15-38.53
6	26	36.92	0.76	0.15	35.24-38.02
Basal length					
Males					
1	55	28.95	0.61	0.08	27.73-30.22
2	14	28.64	0.44	0.12	27.80-29.38
3	50	28.97	0.74	0.10	26.14-30.64
4	23	28.89	0.80	0.17	27.48-30.47
5	19	29.09	0.57	0.13	28.05-30.22
6	25	29.67	0.63	0.13	28.21-30.62
Females					
1	59	29.04	0.85	0.11	27.08-32.22
2	16	28.84	0.91	0.23	27.11-30.48
3	31	28.59	0.78	0.14	27.43-30.76
4	15	28.81	0.64	0.17	27.43-30.08
5	13	29.22	0.89	0.25	27.77-30.91
6	25	29.56	0.73	0.15	28.00-31.02

TABLE 1.—*Continued.*

Group	N	Mean	SD	SE	Range
Length of diastema					
Males					
1	56	8.83	0.32	0.04	8.16-9.49
2	16	8.81	0.31	0.08	8.12-9.42
3	60	8.94	0.29	0.04	8.33-9.64
4	23	8.97	0.36	0.08	8.42-9.78
5	20	9.02	0.32	0.07	8.45-9.76
6	32	9.26	0.25	0.04	8.84-9.77
Females					
1	62	8.83	0.41	0.05	7.77-9.69
2	17	8.90	0.39	0.10	8.09-9.89
3	36	8.76	0.33	0.06	8.08-9.40
4	15	8.83	0.24	0.06	8.23-9.34
5	14	8.90	0.46	0.12	7.89-9.62
6	30	9.16	0.25	0.05	8.62-9.60
Width of upper molars					
Males					
1	56	7.39	0.23	0.03	6.94-7.90
2	16	7.34	0.26	0.06	6.83-7.83
3	60	7.41	0.32	0.04	6.81-9.06
4	21	7.41	0.24	0.05	6.88-7.85
5	20	7.42	0.31	0.07	6.80-7.96
6	32	7.50	0.23	0.04	6.99-7.98
Females					
1	63	7.31	0.34	0.04	5.04-7.84
2	17	7.35	0.30	0.07	6.67-8.09
3	35	7.35	0.23	0.04	6.81-7.90
4	13	7.40	0.18	0.05	7.12-7.77
5	14	7.44	0.22	0.06	7.11-7.78
6	30	7.42	0.23	0.04	7.01-7.93
Length of maxillary toothrow					
Males					
1	56	5.33	0.29	0.04	4.69-5.92
2	16	5.13	0.19	0.05	4.82-5.43
3	60	5.14	0.24	0.03	4.54-5.74
4	20	5.13	0.26	0.06	4.63-5.54
5	20	5.15	0.31	0.07	4.71-5.66
6	32	5.34	0.32	0.06	4.51-5.89
Females					
1	63	5.18	0.29	0.04	4.68-5.69
2	17	5.12	0.33	0.08	4.65-5.57
3	36	5.13	0.30	0.05	4.56-5.78
4	14	5.09	0.28	0.07	4.74-5.69
5	14	5.40	0.46	0.12	4.59-6.17
6	30	5.40	0.32	0.06	4.69-5.90

TABLE 1.—Continued.

Group	N	Mean	SD	SE	Range
Depth of skull					
Males					
1	56	14.10	0.31	0.04	13.32-15.01
2	16	14.00	0.27	0.07	13.55-14.54
3	59	13.99	0.32	0.04	13.10-14.88
4	23	14.10	0.30	0.06	13.59-14.81
5	19	14.01	0.34	0.08	13.28-14.96
6	28	14.12	0.37	0.07	13.20-14.65
Females					
1	63	14.04	0.35	0.04	12.92-14.79
2	17	14.14	0.34	0.08	13.43-14.64
3	33	13.99	0.33	0.06	13.34-14.81
4	14	13.97	0.37	0.10	13.48-14.84
5	14	14.16	0.47	0.13	13.53-15.15
6	30	14.13	0.33	0.06	13.27-14.66
Total length					
Males					
1	43	243.67	10.33	1.53	225-276
2	15	245.33	7.50	1.94	227-259
3	57	236.93	14.57	1.93	199-271
4	22	242.05	14.75	3.14	207-280
5	4	248.75	8.54	4.27	240-260
6	31	244.58	13.71	2.46	200-266
Females					
1	41	244.71	13.63	2.13	215-278
2	15	243.40	13.55	3.50	217-260
3	36	238.94	13.26	2.21	214-270
4	14	234.79	16.92	4.52	187-257
5	5	253.20	11.34	5.07	239-270
6	25	244.36	11.53	2.31	218-265
Length of tail vertebrate					
Males					
1	43	130.70	8.21	1.25	118-156
2	15	129.53	7.00	1.81	118-145
3	56	127.64	11.72	1.57	85-152
4	22	127.27	9.24	1.97	98-142
5	4	132.00	9.09	4.55	120-140
6	31	132.97	9.43	1.69	109-154
Females					
1	41	129.93	11.94	1.86	99-160
2	15	128.67	11.63	3.00	105-150
3	36	130.11	9.10	1.52	103-143
4	14	126.21	16.06	4.29	83-146
5	5	138.40	10.01	4.48	130-155
6	25	131.64	5.89	1.18	120-140

TABLE 1.—Continued.

Group	N	Mean	SD	SE	Range
Length of hind foot					
Males					
1	38	38.63	1.62	0.26	35-41
2	15	38.13	2.17	0.56	34-41
3	57	37.75	2.19	0.29	41-57
4	22	38.55	1.60	0.34	36-43
5	4	38.75	2.63	1.31	35-41
6	31	40.52	2.16	0.39	35-49
Females					
1	36	39.25	2.41	0.40	35-49
2	15	37.80	2.18	0.56	34-42
3	36	37.14	2.11	0.35	33-40
4	14	37.79	1.37	0.37	35-40
5	5	38.00	2.74	1.22	34-41
6	25	40.00	2.60	0.52	35-50
Length of ear					
Males					
1	43	13.37	1.35	0.21	10-18
2	15	12.40	0.91	0.24	11-14
3	57	12.25	1.87	0.25	08-16
4	22	13.59	1.47	0.31	08-15
5	4	13.25	2.36	1.18	10-15
6	31	13.84	1.92	0.34	08-16
Females					
1	41	13.22	1.71	0.27	09-20
2	15	13.53	2.07	0.53	11-19
3	36	12.33	1.87	1.31	07-16
4	14	14.00	1.11	0.30	12-15
5	5	13.80	3.11	1.39	11-19
6	24	13.88	1.83	0.37	08-16

oklahomae, the first two of which are of immediate concern as the focus of this investigation.

Four populations of *D. ordii* from the High Plains of Texas that encompass the ranges of *D. o. medius* and *D. o. richardsoni* (as described by Hall and Kelson, 1959) were examined by Schmidly (1971). Schmidly did not assign subspecific status to these populations, but he did find that one from north of the Canadian River varied significantly when compared to those to the south of the river in 11 of the 14 characters examined. The two most southerly populations varied little from each other, whereas the fourth (Needmore, Bailey County) seemed to lie in a zone of intergradation between the two southernmost populations and the one to the north of the Canadian. Several factors may contribute to reduction of gene flow between northern and southern

populations of Ord's kangaroo rat on the High Plains of Texas and adjacent New Mexico.

First, because the four populations studied by Schmidly were arranged essentially in a north-south direction, spatial separation alone may account for much of the isolation between them. Second, the northern edge of the Llano Estacado (Canadian River breaks) may serve as a barrier to gene flow, and finally the agricultural activity on the Llano may be partially involved in producing divergence among semi-isolated populations (Schmidly, 1971). Schmidly's findings agreed with those of Desha (1967) in suggesting that patterns of variation in *D. ordii* are more complex than previously thought by Setzer (1949), and that there was a need to re-evaluate geographic variation in this species using statistical techniques.

For analysis of geographic variation, specimens from adjacent localities were pooled to form six groups (Fig. 1) of sufficient sample size for statistical analyses. Care was taken not to cross any potential biogeographic barrier in selecting pooled samples. We decided a sample size of 20 individuals (10 males and 10 females) from immediately adjacent localities would be the minimum number necessary before individuals could be pooled. Six pooled groups were formed using that criterion. Three of these groups were from atop the Llano Estacado and three were from adjacent areas. Also, three of the groups were within the presumed range of *D. o. richardsoni* and the remaining three were within the presumed range of *D. o. medius* (as mapped by Hall, 1981). Specimens from adjacent localities that were not in sufficient number to pool were left ungrouped and treated as unknown in subsequent analyses. General location of the six groups follows (see Table 1 for sample sizes).

Group 1—Muleshoe Sand Hills—Bailey, Lamb, and Hale counties

Group 2—Cochran and Yoakum counties

Group 3—Winkler County

Group 4—Lynn County

Group 5—Dickens County

Group 6—Hemphill County

These were tested for the presence of significant geographic variation among groups with a MANOVA. For both males and females, highly significant ($P < 0.001$) differences were obtained, indicating that at least some of the groups were different. The groups then were subjected to one-way ANOVAs on each cranial character with the

TABLE 2.—Results of the Student-Newman-Kuels multiple range test (MRT) on cranial characters that showed significant differences with one-way ANOVAs (similar results were obtained with Duncan and Scheffes). Asterisks (*) in a column indicate homogenous subsets of the groups.

Males			Females		
Group	Means	MRT	Group	Means	MRT
Greatest length of skull					
2	39.27	*	3	39.29	*
5	39.43	*	1	39.39	*
3	39.50	*	4	39.42	* *
1	39.54	*	2	39.51	* *
4	39.76	* *	5	39.76	* *
6	40.03	*	6	40.01	*
Postorbital constriction					
5	12.80	*	NS		
2	12.98	* *			
4	13.02	* *			
6	13.08	* *			
3	13.19	* *			
1	13.37	*			
Maxillary breadth					
2	21.27	*	3	21.04	*
4	21.28	*	4	21.19	* *
3	21.28	*	2	21.33	* *
1	21.46	* *	1	21.58	*
5	21.72	*	5	21.67	*
6	21.74	*	6	21.72	*
Rostral breadth					
4	3.72	*	4	3.77	*
1	3.87	*	1	3.90	*
3	3.90	*	2	3.96	* *
2	3.95	* *	3	3.97	* *
5	4.02	* *	6	4.01	* *
6	4.11	*	5	4.11	*
Length of nasals					
4	14.03	*	4	14.20	*
1	14.47	*	3	14.33	*
3	14.48	*	5	14.43	* *
5	14.52	* *	1	14.52	* *
2	14.56	* *	2	14.54	* *
6	14.89	*	6	14.81	*
Least supraoccipital breadth					
4	2.44	*	4	2.50	*
3	2.49	*	3	2.53	*
1	2.62	* *	1	2.56	*
2	2.77	* *	2	2.75	* *
5	2.77	* *	5	2.86	*
6	2.87	*	6	3.00	*

TABLE 2.—Continued.

Males			Females		
Group	Means	MRT	Group	Means	MRT
Bullar-premaxillary length					
2	36.27	*	NS		
1	36.51	*			
5	36.54	*			
3	36.54	*			
4	36.62	*			
6	37.15	*			
Basal length					
2	28.64	*	3	28.58	*
4	28.89	*	4	28.81	*
1	28.94	*	2	28.87	*
3	28.96	*	1	29.04	*
5	29.08	*	5	29.21	* *
6	29.67	*	6	29.55	*
Length of diastema					
2	8.81	*	3	8.76	*
1	8.82	*	1	8.82	*
3	8.93	*	4	8.82	*
4	8.96	*	5	8.90	*
5	9.01	*	2	8.90	*
6	9.25	*	6	9.16	*
Length of maxillary tooththrow					
2	5.12	*	4	5.08	*
4	5.12	*	2	5.11	*
3	5.14	*	3	5.13	*
5	5.15	*	1	5.18	*
1	5.32	*	6	5.39	*
6	5.34	*	5	5.40	*

pooled geographic localities as the main effect and, if significant differences were present, to *a posteriori* multiple range tests. Finally, a discriminant function analysis (DFA-program DISCRIMINENT) was utilized to ascertain how well the geographic groupings were discriminated from each other as well as to determine to which group the individuals treated as unknown were most closely associated.

Eight of the 13 characters were significant ($P = 0.05$) for both males and females. Additionally, males exhibited significance in postorbital constriction and bullar-premaxillary length ($P = 0.05$), whereas females did not ($P = 0.05$) (see Table 2). Characters found to be significant were then subjected to three multiple range tests (Duncans, Student-Newman-Keuls, and Scheffes) to identify which of the groups formed maximally nonsignificant subsets.

The results of the multiple range tests demonstrated kangaroo rats in group 6 (see Fig. 1) to be significantly different from those in the three groups (1, 2, and 4) from the Llano and group 3 from south of the Llano. Group 5 appeared to be an intermediate group. Groups 1 through 4 formed subsets for seven of 10 characters for males and six of eight characters for females. Rats in group 6 were consistently the largest for most characters (nine of 10 characters for males and six of eight in females), and it was isolated as a subset for three characters (bullar-premaxillary length, basal length, and length of diastema) in males and one in females (diastema). Group 6 was a member of two subsets for only one character in males (postorbital constriction) and females (rostral breadth). *D. ordii* in group 5 constituted the second largest specimens for most of the characters, being identified in overlapping subsets with six and the other groups for four characters in males, and five characters in females, suggesting it is an intermediate group in that it shows some characteristics of both group 6 and the other groups to the south and west. Interestingly, group 4 was the nearest geographically to group 5 but contained the smallest specimens for most mensural characters. Results of Student-Newman-Keuls *a posteriori* multiple range test are presented in Table 2.

The fact that group 6 did not overlap in the majority of the subsets indicates that this group is significantly different from the others. The difference can be attributed partly to the geographic distance from the other groups and also to the fact that 6 is isolated north of the Canadian River and its breaks. Group one, recognized as representing *D. o. richardsoni* by Hall (1981), clearly showed a greater similarity to groups to the south that currently are regarded as *medius*.

The DFA classified males correctly 55 percent of the time or better in all groups except group 3, in which only 26 percent of the individuals were classified correctly. Males and females from group 3 were dispersed relatively evenly among the other groups, suggesting that group 3 represents an heterogenous population. The groups with the highest correct classification were groups 5 and 6, in which 70 and 74 percent were correctly classified, respectively. Females were more heterogenous than males; there were only two groups in which more than 50 percent of the individuals were correctly classified (groups 4 and 6). The results of DFA are presented in Table 3.

Locations of specimens treated as unknown in relation to the pooled groups are shown in Figure 1. Sixty-five percent of all individuals

TABLE 3.—*Results of discriminant function classification using the six sample groups. Columns are the groups into which selected individuals were classified and rows are the groups to which the same individuals belong.*

Group	1	2	3	4	5	6
Males						
1	29	5	4	8	3	4
2	2	8	1	2	1	0
3	6	7	10	6	6	4
4	2	0	2	12	2	1
5	1	0	0	2	12	2
6	1	1	0	0	4	17
Females						
1	23	8	3	15	4	5
2	2	2	5	3	1	3
3	3	6	10	5	2	2
4	2	2	1	6	1	0
5	1	1	1	1	5	3
6	2	4	0	0	4	15

from north of the Canadian River were classified with group 6, with an additional 19 percent assigned to group 5; only four individuals were assigned to groups on the Llano. Individuals obtained from the Llano were classified with groups on the Llano or with group 3 from south of the Llano 55 percent of the time. Specimens from along the eastern margin of the Llano Estacado, on and off the caprock, were divided between groups on the Llano and groups 5 and 6. For example, Garza County samples from on and off the caprock were divided between groups 1 and 3 and 5 and 6. There was no particular pattern in assignment of individuals in that kangaroo rats from both on the caprock and east of it were assigned to groups centered on and off the Llano. However, those individuals from locations farthest east of the Llano were classified primarily with groups 5 and 6. For example, a sample of 13 individuals from Wichita and Wilbarger counties, which are located on the eastern margin of the currently recognized distribution of *D. o. richardsoni*, had only one individual (a female) that was not classified as belonging to group 5 or group 6. Also, individuals from Childress and Collingsworth counties were classified with group 6 almost exclusively. Unknown animals from south of the Llano Estacado were classified with all groups at about the same frequency, probably due the heterogenous nature of these populations as exemplified by group 3.

The results of these data indicate that there is a significant difference between populations of *D. ordii* on the Llano south of the Canadian

River and those to the north, and that these are not members of the same subspecies. Furthermore, populations from south of the Canadian River on the Llano currently recognized as *D. o. richardsoni* (see Hall, 1981) exhibit traits that more closely resemble *D. o. medius*. Kangaroo rats from east of the Llano Estacado exhibit traits similar to those of *richardsoni* even though there is a zone where intermediate individuals occur. It is here proposed that the boundary between the two subspecies in Texas be redefined as the northern and eastern boundaries of the Llano Estacado, and that the subspecific name *medius* be used henceforth to include all populations on the Llano Estacado that previously were referred to as *richardsoni*. Those populations from east of the Llano that previously were referred to as *medius* should be assigned to *richardsoni*. To the southwest, the Llano merges with the Monahans Sand Hills and probably does not pose a barrier to gene flow between kangaroo rats on the Llano and those to the southwest. The southern boundary of the Llano merges with the Edwards Plateau where an area of unsuitable habitat separates populations east of the Llano from those to the southwest, and we propose that this also be recognized as a point of separation between the two subspecies.

ACCOUNTS OF SUBSPECIES

Dipodomys ordii medius Setzer

Dipodomys ordii medius Setzer, Univ. Kansas Publ., Mus. Nat. Hist., 1:519, 1949. Holotype from Santa Rosa, Guadalupe Co., New Mexico.

Distribution.—In Texas, from the northern boundary of the Llano Estacado south at least to the Pecos River, and from eastern New Mexico to the breaks on the eastern margin of the Llano.

Comparisons.—Compared to *D. o. richardsoni*, geographically adjacent to the north and east, *D. o. medius* is smaller in overall external measurements and all cranial measurements except postorbital constriction. Respective means of selected cranial measurements for adult males and adult females are: greatest length skull, 39.41, 39.45; maxillary breadth, 21.37, 21.38; basal length, 28.79, 28.96; and length of diastema, 8.89, 8.82.

Remarks.—Schmidly (1971) noted that specimens from Needmore, Bailey Co., Texas (part of group 1 on Fig. 1), located on the Llano Estacado, were intermediate between specimens from north of the Canadian River and those he examined from localities to the south of Needmore. He did note, however, that the Needmore population was

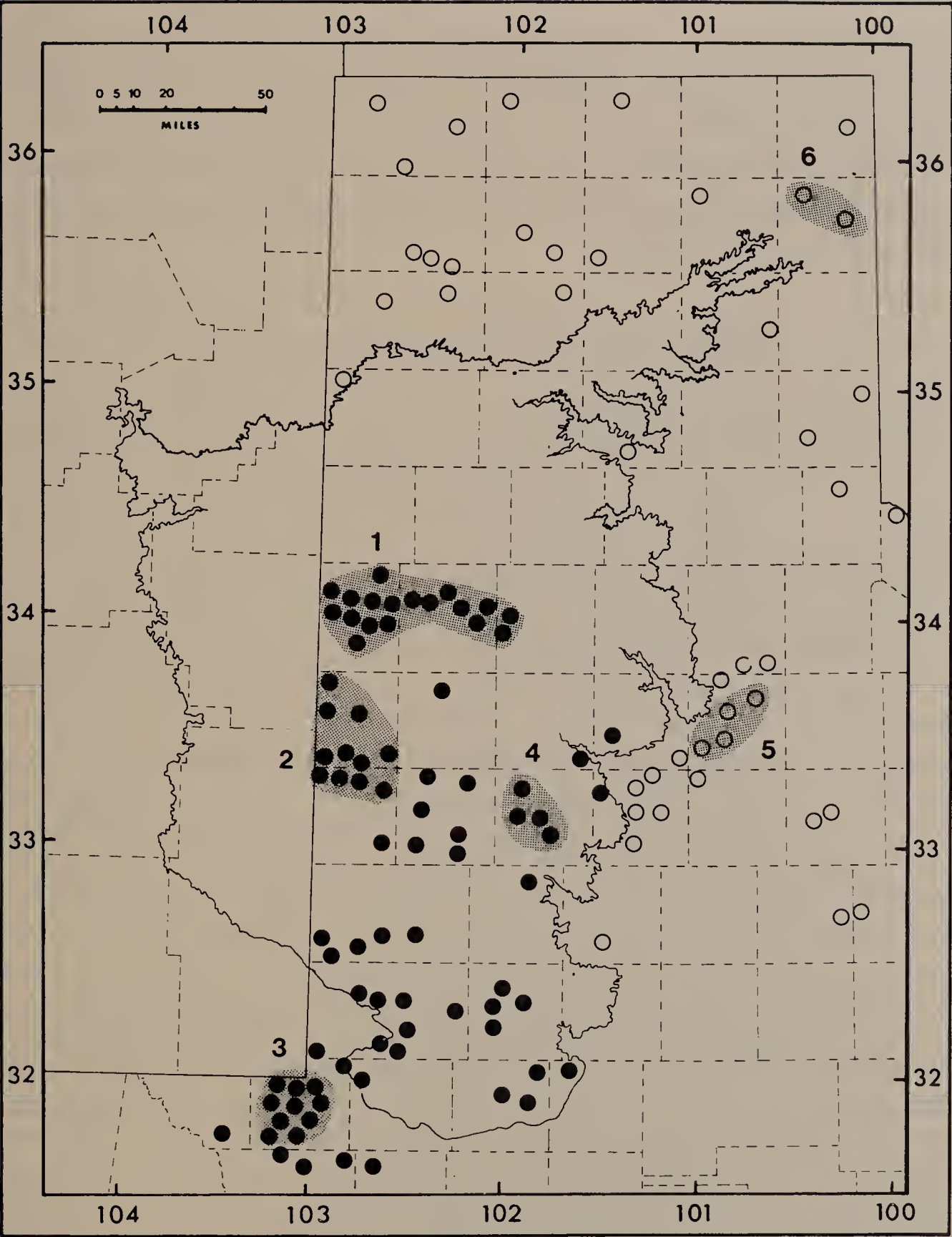


FIG. 1. Map of the Llano Estacado and adjacent regions showing the location of places from which specimens were examined (dots), and the areas encompassed by the six pooled samples (see text). Solid symbols represent *Dipodomys ordii medius*, whereas open symbols denote *D. o. richardsoni*.

significantly different from the population north of the Canadian. Specimens from both locations were examined during this study and specimens from Needmore showed no affinity for samples from north

or east of the Llano. Rats in the sample from the Muleshoe Sand Hills and vicinity resemble *richardsoni* only in maxillary breadth in both males and females and in length of maxillary toothrow in males. Some individuals in group 3 from the Monahans Sand Hills did resemble *richardsoni* in some features, but this population is isolated from that race by the Llano Estacado to the north and the northwestern part of the Edwards Plateau to the east.

Specimens examined.—Total of 920, all from Texas and housed in The Museum of Texas Tech University. ANDREWS CO.: 1 mi. S Frankel City, 1; 1 mi. S, 1 mi. E Frankel City, 2; 4 mi. N, 9 mi. W Andrews, 1; 4 mi. N, 3-5 mi. E Andrews, 4; 3 mi. N, 10-11 mi. W Andrews, 3; 5-6 mi. S, 6 mi. E Andrews, 7; 7 mi. S, 3-4 mi. E Andrews, 3; 8.5 mi. S, 4 mi. E Andrews, 2; 14 mi. S Andrews, 1; 18 mi. N, 2 mi. E Kermit, 2. BAILEY CO.: 7 mi. N Muleshoe, 17; 0.5-2.5 mi. S, 18 mi. W Muleshoe, 4; 2 mi. S, 10 mi. W Muleshoe, 4; 3.2 mi. S, 2.7-3.1 mi. W Muleshoe, 2; 4 mi. SW Muleshoe, 1; 4 mi. S Muleshoe, 1; 4 mi. S, 1-2 mi. W Muleshoe, 15; 4 mi. S, 1 mi. E Muleshoe, 1; 5 mi. S, 18 mi. W Muleshoe, 4; 5.5 mi. S, 10 mi. W Muleshoe, 4; 6 mi. S, 1-3 mi. E Muleshoe, 24; 8.5 mi. S, 16.5 mi. W Muleshoe, 2; 9.5 mi. S, 13 mi. W Muleshoe, 15; 9.5 mi. S, 8.5-9 mi. W Muleshoe, 2; 3.5 mi. N Needmore, 62; 3.5-5.7 mi. S, 2-2.7 mi. W Needmore, 12; Muleshoe Nat. Wildlife Refuge, 6. COCHRAN CO.: 18 mi. W Morton, 2; 1 mi. W Bledsoe, 1; 2 mi. E Lehman, 1; 1-2.5 mi. W FM 1780 on FM 1585, 4; 13 mi. S Lehman, 3; 5 mi. E State Hwy. 214, 6 mi. S FM 1585, 5; 11 mi. N Bronco, 4. CRANE CO.: 17 mi. N, 19 mi. W Crane, 1; FM 1053, 5 mi. S Interstate 20, 1; 5 mi. N, 17 mi. W Crane, 7. CROSBY CO.: 12.5-13.5 mi. S, 1.1-2.1 mi. W Ralls, 8. DAWSON CO.: 9 mi. N, 4 mi. E Lamesa, 2. ECTOR CO.: 4 mi. N Notrees, 1. GAINES CO.: 4 mi. S, 9 mi. E Seminole, 4; 5 mi. S Seminole, 1; 7 mi. S, 10.3 mi. W Seminole, 3; 10 mi. S, 20 mi. W Seminole, 1; *unidentifiable locality*, 1. GARZA CO.: 6 mi. S Southland, 2; *no specific locality*, 1. GLASSCOCK CO.: 0.5 mi. S, 11 mi. W Lees, 2. HALE CO.: 0.5 mi. N, 12 mi. W Hale Center, 1; 4-4.5 mi. N, 5.5 mi. W Cotton Center, 12. HOCKLEY CO.: 10 mi. N, 0.5 mi. W Levelland, 2; 12 mi. N Levelland, 4. LAMB CO.: 4-5.5 mi. S, 2.5 mi. E Earth, 27; 6-6.5 mi. S Springlake, 9; 7.2-7.6 mi. S Earth, 5; 6-7.5 mi. N Sudan, 6; 7 mi. S Olton, 5; 8-8.5 mi. S, 1-2 mi. E Olton, 3; 6.5 mi. N, 0.5 mi. E Fieldton, 1; 3-4 mi. N Fieldton, 30; 14.1 N Littlefield, 1; 10.6 mi. N Spade, 2. LOVING CO.: 2 mi. N, 5 mi. E Mentone, 3; 4.1 mi. E Mentone, 1; 8.5 mi. E Mentone, 2. LUBBOCK CO.: 1 mi. E Tahoka Hwy., 1; 3.5 mi. N Slaton, 1. LYNN CO.: 3 mi. S New Home, 4; 6 mi. W Tahoka, 2; 2.6 mi. W Tahoka, 1; Tahoka, 8; 3.5 mi. S Tahoka, 1; 6.5 mi. SW Tahoka, 3; 7 mi. SW Tahoka, 64; 5 mi. S, 3-4 mi. W Tahoka, 7; 5 mi. S Tahoka, 4. MARTIN CO.: 7 mi. N, 1 mi. E Tarzan, 3; 15 mi. S Flower Grove, 2; 19-19.9 mi. S Patricia, 10; 7 mi. N, 17 mi. W Stanton, 1. MIDLAND CO.: 6.5 mi. S, 1 mi. E Stanton, 2; 7 mi. SE Midland, 1; 5 mi. S, 15 mi. E Midland, 1. TERRY CO.: 3.5 mi. N, 12 mi. W Meadow, 2; 3.5 mi. N, 10 mi. W Meadow, 2; 3 mi. S, 2 mi. E Meadow, 2; 4 mi. N Gomez, 1; 2 mi. S, 8 mi. E Brownfield, 1; 2 mi. N, 3 mi. W Wellman, 1; 1 mi. S Wellman, 1; 10 mi. S Brownfield, 1; 12 mi. S, 2 mi. E Brownfield, 1. UPTON CO.: 3.5 mi. N, 2.5 mi. E Crane, 4. WARD CO.: 8.2-8.6 mi. S Wink, 7; 9.5 mi. S Wink, 6; 9 mi. NE Monahans, 1; 6 mi. NE Monahans, 1; Monahans State Park, 2; 9 mi. W Monahans, 7; 11 mi. WSW Monahans, 1. WINKLER CO.: 10 mi. NW Notrees, 1; 6.7 mi. N, 4 mi. W Notrees, 4; 9.1

mi. NW Kermit, 1; 4.1 mi. N, 5.1 mi. E Kermit, 18; 4 mi. N Kermit, 1; 4 mi. NW Kermit, 1; 2 mi. N, 3 mi. E Kermit, 1; 6 mi. W Kermit, 1; vic. Kermit, 1; 6-6.6 mi. E Kermit, 15; 1.6 mi. S Kermit, 1; 6-6.7 mi. SE Kermit, 52; 7 mi. SW Kermit, 1; 4 mi. S, 3 mi. E Kermit, 2; 2.5 mi. NE Winkler County Airport, 1; Winkler County Airport, 109; 6 mi. S Kermit, 33; 6 mi. S, 2 mi. E Kermit, 71; Wink and localities within 4.5 mi. thereof, 14; 6.5 mi. E Wink, 1; 10 mi. S Kermit, 2; 4.7 mi. S, 0.5 mi. W Wink, 11; 6 mi. S Wink, 3. YOAKUM Co.: 8 mi. N Bronco, 3; 7 mi. N, 6.5 mi. E Bronco, 6; 22.9 mi. S, 3.7 mi. E Lehman, 16; 13-14 mi. N Plains, 16; 9.5 mi. N, 13 mi. E Plains, 1; 6 mi. S, 12 mi. E Plains, 6.

Dipodomys ordii richardsoni (J. A. Allen)

Dipodops richardsoni J. A. Allen, Bull. Amer. Mus. Nat. Hist., 148:317, 1891. Holotype from confluence of Cienquilla and Currumpaw creeks, sec. 32, T. 2 N, R. 2 E, Cimarron Co., Oklahoma (Glass, 1971:498).

Dipodomys ordii richardsoni, Grinnell, J. Mamm., 2:96, 1921.

Distribution. North of the Canadian River breaks that form the northern border of the Llano Estacado, east of the Llano Estacado to the eastern margin of the range of *D. ordii*, and south to the edge of, but not on, the Edwards Plateau.

Comparisons. See account of *D. o. medius*. Means of selected cranial measurements for adult males and adult females are, respectively: greatest length of skull, 40.03, 40.01; maxillary breadth, 21.74, 21.72; basal length, 29.67, 29.55; and length of diastema, 9.25, 9.16.

Remarks.—Although there is no apparent evidence for gene flow between *medius* and *richardsoni* along the northern margin of the Llano Estacado, there is evidence of gene flow between the two races on the eastern margin of the Llano. This may be because the northern boundary between *medius* and *richardsoni* is characterized by inhospitable rocky breaks on both sides of the Canadian River, and the river itself may pose a partial barrier. On the eastern boundary, gene flow may be facilitated by contact through canyons that open off the caprock onto the Rolling Plains to the east. Although *D. ordii* prefers sandy loam soils to deep sandy dunes, Dalquest *et al.* (1990) noted that it is a surprisingly adaptable species. They examined a specimen of *D. o. richardsoni* from an area of extensive volcanic cinders with no apparent soil development, and also noted that a specimen was taken from the north side of Capulin Mountain, New Mexico, in an area with little exposed soil.

Specimens examined.—Total of 435, all from Texas and housed in The Museum of Texas Tech University. ARMSTRONG Co.: 18.5 mi. S, 3 mi. W Claude, 1. BORDEN Co.: 12 mi. S, 1 mi. W Gail, 1. CHILDRESS Co.: 11 mi. N Childress, 1. COLLINGSWORTH Co.:

2 mi. N, 9 mi. E Lutie, 9; 1 mi. N, 9 mi. W Wellington, 2. CROSBY Co.: vic. Crosbyton [White River] Lake, 1; 2 mi. S White Lake Village, 1. DALLAM Co.: 2 mi. N, 13 mi. E Texline, 1; 12 mi. E Texline, 11; 10.6 mi. W Stratford, 1; 1 mi. N, 6 mi. W Dalhart, 1. DEAF SMITH Co.: 4.9 mi. S, 4.8 mi. E Glenrio, 1; 7 mi. S, 3 mi. E Glenrio, 2. DICKENS Co.: 4 mi. S, 5 mi. E Roaring Springs, 2; 6 mi. N, 9 mi. E Dickens, 6; 5 mi. N, 6 mi. E Dickens, 4; 3.5 mi. N Dickens, 1; 5 mi. N Spur, 2; 3 mi. N, 8 mi. W Spur, 7; 7-7.5 mi. S, 10-10.5 mi. W Dickens, 76; 1 mi. E FM 836, 1 mi. N FM 2565, 1. FISHER Co.: 3 mi. E Sylvester, 2; 2 mi. S, 5 mi. E Sylvester, 2. FOARD Co.: 6 mi. E Thalia, 12. GARZA Co.: 23-25 mi. S Crosbyton, 3; 9 mi. N Post, 1; 10 mi. E Southland, 32; 6 mi. N Post, 1; Post, 1; 7 mi. E Post, 1; 14 mi. S, 1 mi. E Post, 2. GRAY Co.: 11 mi. N McLean, 4. HANSFORD Co.: 13 mi. N Gruver, 1. HARDEMAN Co.: 20.3 mi. N Goodlett, 2. HARTLEY Co.: 11 mi. W Channing, 3; 1.5 mi. S, 6 mi. W Channing, 1; 3 mi. S Channing, 9. HEMPHILL Co.: 7 mi. N Canadian, 11; *Gene Howe Wildlife Manag. Area*, 92; 1.5 mi. N, 1.3 mi. E Canadian, 1; 12 mi. E Canadian, 17. HUTCHINSON Co.: 3.5-4.8 mi. NW Sanford, 11; below dam, 1 mi. N, 1 mi. W Sanford, 1. JONES Co.: 13 mi. S, 0.5 mi. W Hamlin, 2. KENT Co.: 26 mi. W Girard, 8. LIPSCOMB Co.: 2 mi. N, 8 mi. E Lipscomb, 3. MOORE Co.: 3 mi. S Dumas, 3; 7 mi. S, 14 mi. E Dumas, 1. MOTLEY Co.: 8 mi. S, 9 mi. E Matador, 3; 3 mi. E Roaring Springs, 8; 25 mi. N Dickens, 1. OLDHAM Co.: 6 mi. W Boys Ranch, 6; 17 mi. N, 1 mi. W Adrian, 1. POTTER Co.: 4 mi. S, 6 mi. W Fritch, 1; 7 mi. S, 7 mi. W Fritch, 4. ROBERTS Co.: 13-16 mi. S, 11 mi. E Spearman, 19. SHERMAN Co.: 10 mi. N Stratford, 2. STONEWALL Co.: 2 mi. E Swenson, 1; 0.5 mi. S, 0.5 mi. E Peacock, 2. WICHITA Co.: 10 mi. N Electra, 2; 7.5 mi. N, 2 mi. E Electra, 2; 1-4 mi. NW Bruckburnett, 4. WILBARGER Co.: 15 mi. N, 1 mi. E Vernon, 4; 5 mi. N, 6 mi. W Vernon, 13; 2 mi. N, 1 mi. E Elliot, 3.

Discussion

The characteristics of two subspecies of *Dipodomys ordii* on the Llano Estacado and in adjacent areas of Texas have been examined and redefined. The two are differentiated principally on the basis of cranial dimensions. Specimens from north of the Canadian River are significantly larger than those from the Llano Estacado to the south, indicating that populations in these two areas are effectively isolated from each other. The Canadian River itself does not appear to be a hindrance to gene flow in the area to the east of the Llano because there are no significant differences between specimens from the two sides of the river there. Kangaroo rats from south of the river near the Oklahoma border as well as those from near the eastern boundary of the distribution of *D. o. richardsoni* in Texas clearly should be classified with *richardsoni*, showing little if any affinity to *medius*.

There is a zone of intergradation recognized along the southern part of the eastern boundary of the Llano. Those specimens from east of the Llano are now recognized as *richardsoni*; they average larger than rats from the Llano. Those specimens from atop the Llano that previously

were assigned by Setzer (1949) to *richardsoni* are herein recognized as *medius*.

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